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Contrasting responses of springtails and mites to elevation and vegetation type in the sub-Arctic

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ABSTRACT

Climate change is affecting the species composition and functioning of Arctic and sub-Arctic plant and soil communities. Here we studied patterns in soil microarthropod (springtails and mites) communities across a gradient of increasing elevation that spanned 450 m, across which mean temperature declined by approximately 2.5 °C, in sub-Arctic Sweden. Across this gradient we characterized microarthropod communities in each of two types of vegetation, i.e., heath and meadow, to determine whether their responses to declining temperature differed with vegetation type. Mite abundance declined with increasing elevation, while springtail abundance showed the opposite response. Springtail communities were dominated by larger species at higher elevation. Mite abundance was unaffected by vegetation type, while springtail abundance was 53% higher in the heath than meadow vegetation across the gradient. Springtails but not mites responded differently to elevation in heath and meadow vegetation; hemi-edaphic species dominated in the heath at higher elevation while epi-edaphic species dominated in the meadow. Our results suggest that sub-Arctic mite and springtail communities will likely respond in contrasting ways to changes in vegetation and soil properties resulting from climate warming.

1. Introduction

Arctic regions are subject to some of the greatest warming rates on earth, resulting in potentially large changes in vegetation composition, soil communities and soil process rates (AMAP, 2011; Elmendorf et al., 2012; Hartley et al., 2012), all of which could feed back to climate change (Macias-Fauria et al., 2012; Pearson et al., 2013). Understanding the response of each ecosystem component to warming is therefore crucial for understanding future global climate change. Microarthropods, such as springtails (Collembola) and mites (Acari), are major soil biotic drivers of soil nutrient and carbon cycling (Filser, 2002; Seastedt and Crossley, 1980) and changes in their abundance and community composition can greatly affect decomposition rates (Wall et al., 2008). Several experimental climate manipulations aimed at quantifying microarthropod responses to climate warming scenarios have been performed, but these are often relatively short-term (Bokhorst et al., 2008; Convey et al., 2002; Hodkinson et al., 1998; Kardol et al., 2011; Makkonen et al., 2011) and the methodologies can have drawbacks in terms of realism (such as altering the frequency of temperature extremes) or affect multiple microclimate conditions (e.g., moisture deficits, wind speed and shade). This can make it difficult to determine the nature of causality behind response variables (Bokhorst et al., 2013b). Elevational gradients are an alternative approach to quantify climate change effects as they encompass temperature gradients and allow assessment of ecological responses over much larger temporal and spatial scales than is possible through experimental manipulations (Sundqvist et al., 2013). Although many studies have explored the responses of aboveground organisms to elevation (see reviews of Hodkinson, 2005; Sundqvist et al., 2013), fewer have studied whether belowground organisms show similar responses (e.g., Jarvis et al., 2015; Nash et al., 2013; Veen et al., 2017).

Studies that have considered how springtail and mite communities

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Table 1
Soil temperature variables (mean with SE in brackets) in response to elevation (E: 450 m, 700 m and 900 m) and vegetation type (V: heath and meadow) and ANOVA results (*F*-values). Values are mean of five replicate measurements. Numbers within columns followed by different letters are significantly different (Tukey HSD): * < 0.05, ** < 0.01, *** < 0.001. Data was recorded during September 2012 to September 2013 and is derived from Veen et al. (2017).

	Mean annual T (°C)	Degree day sums	Minimum T (°C)	Maximum T (°C)	Temperature range	Freeze-thaw cycles
Heath vegetation						
450 m	2.2 (0.1)^{a}	982 (49)^{a}	−2.1 (0.5)^{a}	12.9 (0.6)	15.0 (1.1)^{a}	10 (4)
700 m	0.2 (0.2)^{b}	808 (38)^{b}	−9.0 (0.9)^{b}	13.6 (1.1)	22.6 (1.7)^{bc}	3 (1)
900 m	0.3 (0.1)^{b}	818 (46)^{b}	−7.3 (0.3)^{b}	13.0 (0.9)	20.3 (1.2)^{abc}	3 (1)
Meadow vegetation						
450 m	3.0 (0.1)^{a}	1266 (63)^{a}	-2.0 (0.6)^{a}	14.9 (0.8)	16.9 (1.3)^{a}	7 (2)
700 m	2.3 (0.5)^{a}	1064 (71)^{b}	-2.7 (0.8)^{a}	14.5 (0.5)	17.2 (0.9)^{ab}	5 (4)
900 m	0.2 (0.5)^{b}	909 (37)^{b}	-9.3 (1.3)^{b}	17.4 (1.2)	26.6 (2.5)^{c}	8 (2)
ANOVA (*F*-values)						
$V_{(1,17)}$	35.4 ***	32.3 ***	6.0 *	9.9 **	0.5	1.2
$E_{(2,17)}$	52.8 ***	13.5 ***	30.7 ***	0.8	12.2 ***	1.9
$V \times E_{(2,17)}$	8.9 **	2.1	14.0 ***	1.7	7.7 **	1.6

respond to elevational gradients show great variability in the response of abundance and richness to elevation (e.g., Hasegawa et al., 2006; Illig et al., 2010; Lamoncha and Crossley, 1998; Nash et al., 2013; Sadaka and Ponge, 2003). These contrasting responses may be due to variation among different elevational gradients in such factors such as vegetation or soil type, precipitation, snowfall, elevational range, and temperature range and extremes, all of which affect microarthropod traits and distribution patterns (Hodkinson, 2005). Vegetation characteristics determine soil properties and food supply for soil microarthropods, thereby affecting their growth and reproduction (Maunsell et al., 2013; Wardle et al., 2004). Vegetation can also promote a spatially heterogeneous environment that selects for a community dominated with sexually reproductive (versus asexually reproductive) taxa (Becks and Agrawal, 2010), which could allow for stronger evolutionary adaptability to environmental changes. Vegetation also greatly affects soil insulation and therefore the soil thermal regime for ectothermic organisms such as microarthropods (Bråten et al., 2012; Kennedy, 1999). As such, vegetation cover mediates temperature extremes at the soil surface (Graae et al., 2012; Shreve, 1924; Walton, 1982); greater temperature extremes may select for microarthropods with life history characteristics such as larger body size and thermal acclimation abilities (Leinaas, 1983; Sømme, 1989; van Dooremalen et al., 2013; Zettel, 2000). In particular, snow is an important insulator against winter freezing and a sufficiently thick snowpack (ca. 20 cm) can greatly insulate the soil against very low ambient temperatures (Bokhorst et al., 2016; Sturm et al., 1997). Therefore, a reduction in snow thickness can strongly affect microarthropod communities due to increased freezing intensity (Bokhorst et al., 2012, 2013a; Coulson et al., 2000; Slatyer et al., 2017). Microarthropod community patterns along elevational gradients are therefore mediated by a complex interplay between vegetation composition and temperature regime, and these may not necessarily change consistently with elevation.

In the present study, we explored how springtails and mites responded to elevation for each of two highly contrasting types of vegetation, i.e., heath and meadow, along an elevational gradient ranging from 450 m to 900 m in sub-Arctic Sweden. Mean summer soil temperature differs by about 2.5 °C between the lowest and highest elevations of this gradient for both vegetation types (Veen et al., 2017). The heath vegetation is dominated by typical tundra dwarf shrub species such as *Vaccinium vitis-idaea*, *V. uliginosum, Empetrum hermaphroditum* and *Betula nana* and the soil has a high organic matter content, with a low pH (4.5) and a high ratio of soil fungi to bacteria (Veen et al., 2017). In contrast, the meadow vegetation is dominated by graminoids and herbs and the soil contains less organic material, has a higher pH (5.5) and supports a lower ratio of fungi to bacteria (Veen et al., 2017). As soil organic matter content and fungal biomass are important resources for most soil microarthropods (Filser, 2002; Illig et al., 2010), we expected higher soil microarthropod abundance in heath vegetation than in meadow vegetation. By comparing the soil microarthropod responses between two contrasting vegetation types we aimed to better understand which factors play a dominant role as potential drivers of soil community composition along elevational gradients.

We tested three hypotheses. First, we hypothesized that microarthropod abundance and richness would decline with increasing elevation due to lower temperatures and increasing soil temperature variability in our study system. Second, we hypothesized that the microarthropod community would become dominated by larger and surface-dwelling species with sexual reproduction at higher elevations. This is because larger surface-dwelling microarthropod species tend to have better thermal acclimation capabilities that enable them to cope with the colder conditions encountered at higher elevations (van Dooremalen et al., 2013; Zettel, 2000). Third, we hypothesized that the heath vegetation would support higher microarthropod abundance due to the thicker soil organic layer (Filser, 2002; Wall et al., 2008), and that this difference between vegetation types persists with increasing elevation. Together, addressing these hypotheses will increase our understanding of how changing temperatures influence soil microarthropod communities in sub-Arctic landscapes and how this effect is mediated by vegetation type.

2. Materials and methods

The study was conducted along an elevational gradient ranging from 450 m to 900 m elevation on the north-east facing slope of Mt Suorooaívi (1193 m a.s.l.), approximately 20 km south-east of Abisko in sub-Arctic Sweden (68°21′N, 18°49′E). For this gradient, mean annual temperature declines with elevation from about 2.5 °C at 450 m to close to 0 °C at 900 m (Table 1). The gradient starts in open birch forest (*Betula pubescens* ssp. *czerepanovii*) at 450 m while the sites at 700 m and 900 m are in open tundra. These vegetation changes integrate the ecosystem and soil characteristics that result from climate differences along the elevational gradient. Along this gradient there are two distinct vegetation types that occur at all elevations, i.e., heath vegetation and meadow vegetation. Based on previous findings from this study system, we know that changes in soil nutrient concentrations, notably phosphorus (Vincent et al., 2014), and organic matter content (Veen et al., 2017) increased consistently with elevation in the heath but not in the meadow (Table S1).

Soil sampling for the present study was done at each of three elevations (450 m, 700 m and 900 m) for each of the two vegetation types. The sampling sites at 450 m were within open birch forest (*Betula pubescens* ssp. *czerepanovii*), while the sites at 700 m and 900 m were above the tree line. The sampling points were within 50 cm of the study plots of previous work done on vegetation and soil characteristics along

this gradient by Veen et al. (2017). Our sampling was done at locations with the same vegetation composition as the plots used by Veen et al. (2017) to ensure that the plant effects on soil properties would be comparable. For each vegetation type at each elevation, 10 replicate soil samples (10 cm diameter, 8 cm deep which included the organic layer and top of the mineral layer) were randomly taken during 2–3 July 2012 within a 50 m × 50 m area where the vegetation was dominated by the representative plants of the target vegetation type at that elevation. The mean distance between samples within elevations was ca 10 m with the maximum distance between the two samples furthest apart being ca 50 m. Considering the high level of heterogeneity in soil properties (such as, nitrogen mineralization) and vegetation over short distances observed in this study system (Björk et al., 2007), this distance is sufficient to ensure independence between sampling points. Upon collection, soil cores were stored in closely fitting plastic containers, and were kept at 5 °C for 3 days before extraction using Tullgren extractors for 3 weeks (van Straalen and Rijninks, 1982). Extracted animals were preserved in 70% ethanol. Springtails were identified to species or genus level, following Fjellberg (1998, 2007). Mites were identified to three major taxonomic groups: Mesostigmata, Oribatida, and a rest group containing Prostigmata and Astigmata.

Soil temperature was measured at 3 cm soil depth at 3 h intervals for a full year from September 2012 to September 2013, at five points for each vegetation type at each elevation (Veen et al., 2017); these five points corresponded to five of the ten points used for soil sampling for microarthropods. These data were used to calculate annual and monthly mean temperatures, degree day sums (> 0 °C), the number of freeze-thaw cycles (the frequency of temperature dropping below 0 °C), and minimum and maximum temperatures. Degree day sums summarize the thermal energy availability for ectothermic organisms, and play a strong role in growth, reproduction and locomotion of soil invertebrates (Addo-Bediako et al., 2002; Birkemoe and Leinaas, 1999). The frequency of freezing and thawing of the soil and minimum and maximum temperatures in a habitat, affected by snow thickness and vegetation cover, provide an indication of its thermal stress and can act as a filter for survival (Block, 1990; Cannon and Block, 1988).

To identify changes in community life history characteristics of springtails between vegetation types and with elevation, we calculated community-weighted mean (CWM) values, separately for each soil sample, based on the approach of Fortunel et al. (2009) and Garnier et al. (2007). For each sample, the relative abundance of each springtail species present was multiplied with its trait value (i.e., body length) and this was summed for all the taxonomic units present to provide the CWM body length. Microarthropod length measures were obtained from literature (Fjellberg, 1998, 2007) and personal archives (S. Bokhorst).

Further, the springtail species were each grouped into one of three categories based on their vertical distribution: epi-edaphic (living on top of the soil), hemi-edaphic (living among the litter layers) and eu-edaphic (living in the soil). These categories incorporate a large suite of traits related to thermal acclimation, mobility and association across the litter and deeper soil layers (Berg et al., 1998; Gisin, 1943; van Dooremalen et al., 2013). Eu-edaphic, hemi-edaphic and epi-edaphic species were given a trait score of 1, 2 and 3, respectively (Bokhorst et al., 2012). For each sample, the relative abundance of each springtail species present was multiplied by its trait value, and this was summed for all the species present to provide the CWM of their vertical distribution. Low CWM vertical distribution values indicate a dominance of soil-dwelling species and represent adaptations to deeper soil conditions, while high values indicate a dominance of surface-dwelling species and represent adaptations to living in the litter layer with larger temperature variability (van Dooremalen et al., 2013). Assignment of springtail species to the different groups, which is based on colour intensity, number of ocelli and literature data on vertical distribution, is presented in Table S2.

To determine biomass of springtails per unit area for each sample, we calculated total springtail biomass in the sample by multiplying the abundance of each species/genus with its estimated body mass, and then summed this for all taxa present. Biomass information of each individual species was obtained from the literature (Caballero et al., 2004; Fjellberg, 1998; Kuznetsova, 2003; Petersen, 1975). In addition, we compared the proportional contribution of sexual versus asexual reproductive strategies in each sample. Data on reproductive strategies were obtained from (Fjellberg, 1998, 2007).

2.1. Statistical analyses

Micro-arthropod response variables were subjected to Analysis of Variance (ANOVA), with vegetation type (heath and meadow) and elevation (450 m, 700 m, and 900 m), and their interaction as fixed factors and with individual samples serving as replicates. The response variables for the springtails included: total abundance, abundance of functional groups (epi-edaphic, hemi-edaphic and eu-edaphic), and abundance of individual species/genera, as well as species/genus richness (hereafter defined as springtail richness), Shannon's-diversity (H'), CWM (length and vertical distribution) values, biomass and the proportion of springtails that have sexual reproduction. For the mites, the response variables included: total abundance and abundance of major groups. We used Tukey HSD tests at $P = 0.05$ to identify differences in means between elevations whenever the effect of elevation or its interaction with vegetation was significant according to ANOVA. In addition, Principal Component Analyses (PCA) was used to summarize the springtail species/genera into fewer variables (using relative abundance), and the first (PC1) and second (PC2) axis scores were compared across vegetation type and elevation using ANOVA as described above. Log-transformations were applied to abundance data to improve homogeneity of variance and this was confirmed using Levene's test. We did not perform formal statistical tests to correlate site characteristics with the microarthropod data because the samples for microarthropods were collected outside the vegetation plots used in Veen et al. (2017). All analyses were performed using SPSS 22.0 for Windows (SPSS Inc., Chicago, IL, USA).

3. Results

3.1. Temperature patterns along the elevational gradient

Mean and minimum soil temperatures and degree day sums were highest, and the temperature range was lowest, at 450 m for both vegetation types (Table 1). All temperature variables indicate that the soils for the meadow vegetation were overall warmer than for the heath. However, mean and minimum temperatures and temperature range also showed significant interactions between vegetation type and elevation (Table 1). As such, the 450 m site was significantly warmer than both the 700 and 900 m sites for the heath vegetation, while sites at 450 m and 700 m were both significantly warmer than the 900 m site for the meadow vegetation (Table 1). The coldest sites also had the largest temperature range and lowest minimum temperatures, indicative of insufficient insulation by snow. There was no significant effect of elevation or vegetation on the number of freeze-thaw cycles.

3.2. Springtail community

Total springtail abundance was overall 53% higher in the heath vegetation than in the meadow vegetation. Springtail abundance was lowest at 450 m in the heath and 450 m and 700 m in the meadow vegetation (Fig. 1, Table 2). The largest change in abundance occurred between 450 m and 700 m for the heath vegetation and between 700 m and 900 m for the meadow vegetation. The abundance of epi-edaphic (surface-dwelling) springtails did not differ between vegetation types, but was highest at 900 m for the meadow vegetation (Fig. 1a, Table S2).

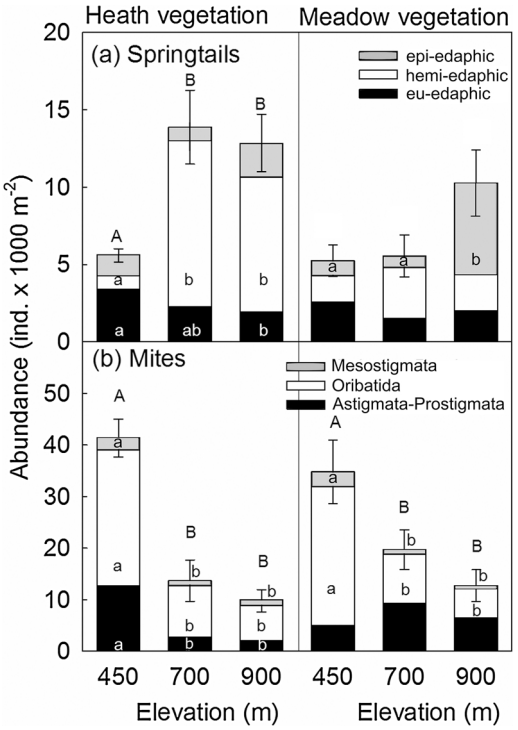

Fig. 1. Abundance of springtails (a) and mites (b) in heath and meadow vegetation along an elevational gradient (450 m, 700 m and 900 m a.s.l.) in sub-Arctic Sweden. Bars are mean of N = 10 replicates with SE as error bars. Within each panel, bars topped with different capital letters differ significantly in total springtail or mite abundance, and for each springtail or mite group, bars associated with different lower-case letters differ significantly (Tukey HSD $P < 0.05$). Accompanying ANOVA statistics are presented in Tables 2 and S2.

Hemi-edaphic (litter-dwelling) springtail abundance was overall higher (177%) in the heath than in the meadow vegetation; their abundance was lowest at 450 m in the heath vegetation, but unresponsive to elevation in the meadow (Fig. 1a). The abundance of eu-edaphic (soil-dwelling) springtails was overall higher (24%) in the heath than in the meadow vegetation and declined with elevation for the heath vegetation, but not for the meadow vegetation (Fig. 1a). Species-specific abundances across both elevation and vegetation types are shown in Table S2.

Springtail species richness did not differ significantly between vegetation types, although species richness was almost significantly ($P = 0.065$) higher in the meadow vegetation (mean ± SE = 8.4 ± 0.4) than in the heath (7.3 ± 0.4); richness was unresponsive to elevation (Table 2). Springtail diversity (H') did not differ between vegetation types, but declined with elevation from 1.8 (± 0.1) at 450 m to 1.5 (± 0.1) at 900 m in the heath vegetation and from 1.7 (± 0.1) at 450 m to 1.4 (± 0.1) at 900 m in the meadow vegetation. The PCA revealed that springtail communities were responsive to both vegetation and elevation (Table 2). PC1 separated the 450 m sites from the higher elevation sites in the heath vegetation while PC2 did this for the meadow vegetation (Fig. 2). The heath communities at 700 m and 900 m were dominated by the hemi-edaphic *Folsomia quadrioculata*. The 450 m sites were dominated by eu-edaphic species such as *Isotomiella minor*, while the meadow springtail community at 900 m was dominated by epi-edaphic springtails *Isotoma anglicana* and *I. viridis*.

Community-weighted mean (CWM) body length of springtails did not differ between vegetation types, but was lowest at 450 m in both vegetation types (Fig. 3a, Table 2). The CWM vertical distribution values were overall higher in the meadow (2.08 ± 0.07) than the heath vegetation (1.86 ± 0.05) and CWM values were higher at 900 m than at 450 m for both vegetation types (Fig. 3b). Total springtail biomass was

Table 2
ANOVA statistics (F and P values) of microarthropod abundance and community level measures in response to elevation (450 m, 700 m and 900 m) and vegetation type (heath and meadow). PC1 and PC2 are the first and second axes derived from Principal Component Analyses. CWM: Community weighted mean value. Reproductive mode refers to the proportional contribution of sexual reproduction (versus asexual reproduction) within the springtail community.

	Elevation (E)		Vegetation type (V)		E × V	
	$F_{(2,54)}$	*P*	$F_{(1,54)}$	*P*	$F_{(2,54)}$	*P*
Springtails						
Total springtail abundance	6.8	0.002	12.0	0.001	2.6	0.084
Total epi-edaphic abundance	11.5	< 0.001	2.0	0.160	4.9	0.011
Total hemi-edaphic abundance	17.6	< 0.001	20.6	< 0.001	6.6	0.003
Total eu-edaphic abundance	3.8	0.028	5.0	0.029	0.0	0.999
Change in total abundance	4.3	0.045	1.8	0.183	31.3	< 0.001
Species richness	0.7	0.496	3.6	0.065	0.2	0.826
Diversity (H')	8.6	0.001	0.5	0.467	3.1	0.055
PC1	22.8	< 0.001	19.1	< 0.001	10.9	< 0.001
PC2	50.3	< 0.001	14.4	< 0.001	10.7	< 0.001
Springtail biomass	34.3	< 0.001	6.0	0.018	6.4	0.003
CWM-length	27.3	< 0.001	1.7	0.196	8.9	< 0.001
CWM-vertical distribution	21.2	< 0.001	11.2	0.001	4.4	0.016
Reproductive mode	30.9	< 0.001	0.1	0.748	0.4	0.664
Mites						
Total mite abundance	14.2	< 0.001	0.0	0.990	1.3	0.277
Total Astigmata-Prostigmata	6.6	0.003	1.5	0.220	6.2	0.004
Total Oribatida	14.7	< 0.001	0.1	0.733	0.6	0.560
Total Mesostigmata	16.0	< 0.001	3.4	0.071	2.7	0.077
Change in total abundance	13.9	< 0.001	5.0	0.031	6.3	0.017

overall 16% higher in the heath vegetation compared to the meadow vegetation (Fig. 3b, Table 2). Springtail biomass was lowest at 450 m in the heath vegetation and at both 450 m and 700 m for the meadow vegetation (Fig. 3c). The proportion of species of springtail that were sexually reproductive did not differ between vegetation types, but was lowest at 450 m (Fig. 3d).

3.3. Mite community

Total mite abundance did not differ between vegetation types and the highest abundance was found at the lowest elevation (Fig. 1b, Table 2). The largest abundance decrease occurred between 450 m and 700 m and this decrease was greater for the heath (67%) than for the meadow vegetation (43%). The three main mite groups did not differ in abundance between vegetation types but did differ between elevations (Fig. 1b, Table S3). Total Astigmata-Prostigmata abundance was highest at 450 m in the heath vegetation but was unresponsive to elevation in the meadow vegetation. Total Oribatida abundance was highest at 450 m for both vegetation types. Total Mesostigmata abundance was at least twice as high at 450 m compared to the other elevations for both vegetation types.

4. Discussion

The springtail and mite communities both showed large but contrasting responses to this elevational gradient. High springtail abundances were generally observed at higher elevations, but the pattern of

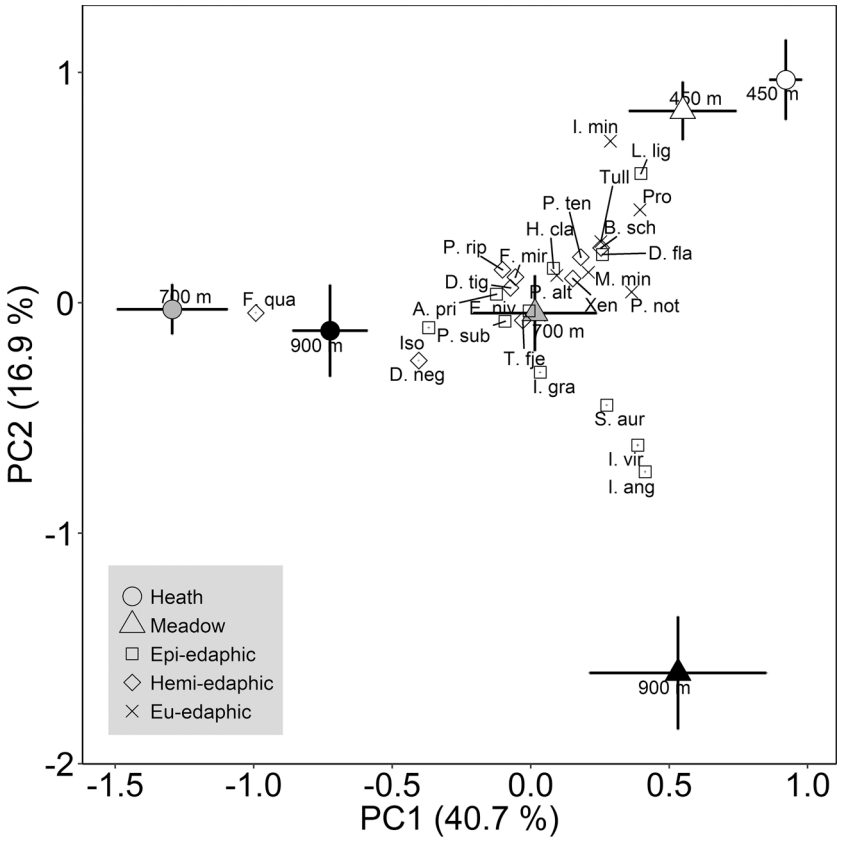

Fig. 2. Ordination biplot from the Principal Component Analysis (PCA) of springtail communities along an elevational gradient with sampling sites at 450 m (white), 700 m (grey) and 900 m a.s.l. (black) in heath and meadow vegetation (circles and triangles, respectively) in sub-Arctic Sweden. The heath and meadow data points for each elevation are the mean of 10 replicate samples, with SE as error bars. Species are grouped by vertical stratification and are indicated by genus (first letter) and species (first three letters) abbreviation. A. pri = *Arrhophalitida principalis*, B. sch = *Ballustura schoettie*, D. fla = *Dicyrtomina flavosignata*, D. neg = *Desoria neglecta*, E. niv = *Entomobrya nivalis*, F. mir = *Friesia mirabilis*, F. qua = *Folsomia quadrioculata*, H. cla = *Heterosminthurus claviger*, Iso = Isotomidae sp, I. ang = *Isotoma anglicana*, I. gra = Isotoma graminis, I. min = *Isotomiella minor*, I. vir = *Isotoma viridis*, L. lig = *Lepidocyrtus lignorum*, M. min = *Megalothorax minimus*, P. not = *Parisotoma notabilis*, P. rip = *Proisotoma ripicola*, P. alt = *Pseudoanuraphorus alticola*, P. ten = *Proisotoma tenella*, Pro = *Protaphorura* sp., S. aur = *Sminthurinus aureus*, T. fje = *Tetracanthella fjellbergi*, Tull = Tullbergidae., Xen = *Xenyllodes armatus*. Accompanying ANOVA statistics relating to PC scores to elevation and vegetation type are shown in Table 2.

the response varied with vegetation type. For the mite community, major declines in abundance occurred between 450 m and 700 m, which coincides with the transition from birch forest to open heath and meadow tundra. Our results suggest that sub-Arctic springtail and mite abundance responses to higher temperatures (i.e., those associated with low elevations) and corresponding shifts in soil properties and

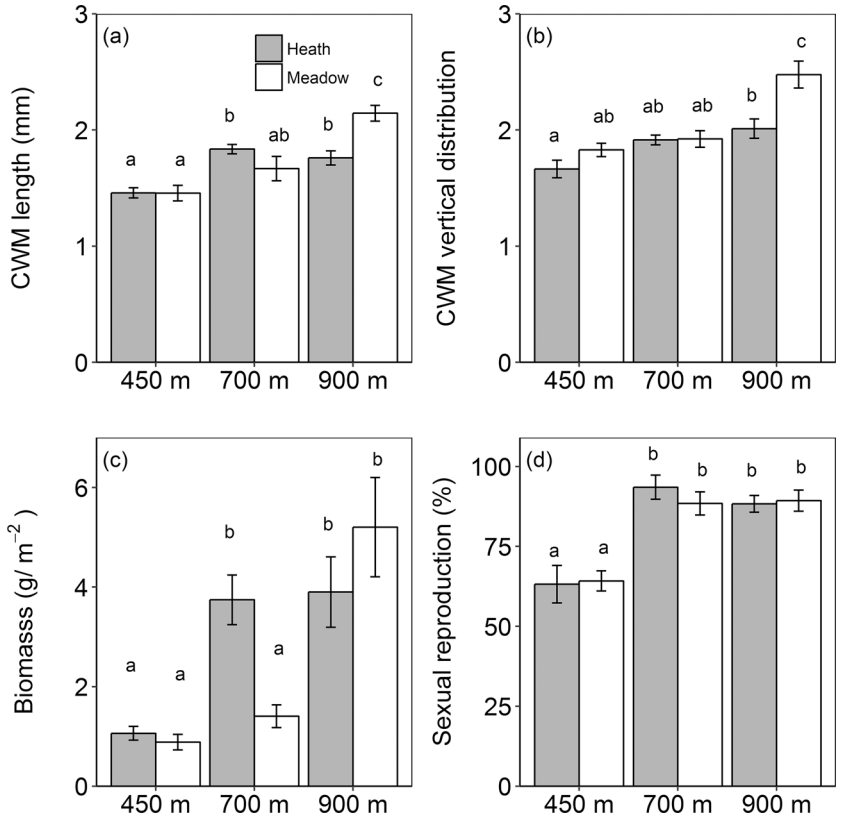

Fig. 3. Community-weighted mean (CWM) measures of springtail length (a), springtail vertical distribution (b), biomass (c) and sexual reproduction (d), in heath and meadow vegetation along an elevational gradient (450 m, 700 m and 900 m a.s.l.) in sub-Arctic Sweden. Bars are mean of N = 10 with SE as error bars. Within each panel, bars topped with different letters differ significantly (Tukey HSD $P < 0.05$). Accompanying ANOVA statistics are shown in Table 2.

vegetation composition may develop in contrasting directions.

Springtail diversity declined along this elevational gradient, which is in line with our prediction as well as other studies of microarthropods along elevational gradients (Cutz-Pool et al., 2010; Illig et al., 2010). However, in contrast to our expectations, springtail abundance was lowest in the birch forest that has high litter inputs and warmer soils, while highest springtail abundance was found in the high elevation tundra where minimum temperatures were coldest. As fungal feeders, springtails could have responded to changes in the fungal species composition that can occur with elevation (Jarvis et al., 2015), given that fungal groups vary in their impact on springtail reproduction and growth (Klironomos et al., 1999). However, our highest elevation sites have many similarities to cold high-latitude regions and glacier forefronts that are often found to support high springtail abundance (Block et al., 2009; Bokhorst et al., 2008, 2017; Janetschek, 1949). High springtail densities in those systems are assumed to be driven by a greater abundance of pioneer species (r-strategists) of diatoms, algae and mosses that function as food sources (Hågvar and Pedersen, 2015; Worland and Lukešová, 2000), and as these are common in low temperature systems (Block et al., 2009), they could also be more abundant at higher, colder elevations.

Mite abundance declined along this elevational gradient, which was in line with our first hypothesis. High mite abundance was found at the lowest elevation (i.e., below the tree line) for both vegetation types, and this probably reflects the more favorable habitat conditions in low elevation open birch forest and tundra with high birch litter input, faster decomposition rates, greater soil porosity and more palatable fungal species when compared with either the heath or meadow vegetation above the tree line (Churchland and Grayston, 2014; Hartley et al., 2012; Jarvis et al., 2015; Nielsen et al., 2012; Sjögersten and Wookey, 2005,2009). In addition, soil mineral PO_4-P concentrations declined with increasing elevation across this gradient (Vincent et al., 2014), which could have negatively affected mite abundance through reduced substrate quality (Hasegawa et al., 2006).

In line with our second hypothesis, springtail communities at higher elevation along this elevational gradient were dominated by larger-bodied species that are associated with the soil surface. These changes in the springtail community along this gradient were driven by large increases in abundance of hemi- and epi-edaphic species and reductions or losses of several smaller eu-edaphic species. Comparable changes in springtail communities have also been reported from within bryophyte communities along elevational gradients in Mexico (Cutz-Pool et al., 2010). In addition, the dominant high elevation springtail species in our study (i.e., *Arrhopalites principalis*, *Isotoma anglicana* and *Folsomia quadrioculata*) occur in high abundances in the high Arctic Svalbard archipelago, suggesting some potential parallels between springtail responses to high elevations and high latitudes (Coulson, 2007; Fjellberg, 2007). The decline of smaller eu-edaphic springtails observed along this elevational gradient was likely driven by their inability to cope with the colder temperatures and greater temperature fluctuations at higher elevations created by a thinner snow pack (Bokhorst et al., 2012; van Dooremalen et al., 2013). There was also a higher proportion of springtail species that were sexually reproductive as elevation increased for both vegetation types. This mode of reproduction tends to be beneficial under more spatially heterogeneous environments (Becks and Agrawal, 2010), while asexual reproduction may be beneficial for soil dwelling species as it is more difficult to find a mating partner in soil. The greater abundance of the large-sized springtails at higher elevations was also likely related to harsher microclimatic conditions (Block et al., 2009) or changes in food availability (Hågvar and Pedersen, 2015). Overall there appears to be a selection against small microarthropod body size and asexual reproduction with colder temperatures across this elevational gradient.

In line with our third hypothesis, springtail abundance and biomass were higher in heath than meadow vegetation, probably because of greater SOM content, total fungal biomass and moss cover in heath vegetation (Bokhorst et al., 2014; Filser, 2002; Veen et al., 2017). In addition, there were significant interactive effects between vegetation and elevation for the springtail communities. However, SOM content, fungal biomass and moss cover did not change with elevation across both vegetation types in a way that would explain the observed changes in springtail abundance and community composition. In addition, while most species were present in both vegetation types, different springtail species were responsible for the change in abundance with elevation in heath versus meadow. The dominance of the litter-dwelling (hemi-edaphic) springtail *Folsomia quadrioculata* in high elevation heath (i.e.,700 m and 900 m) may be associated with the high SOM content (Table S1) or a change in fungal community composition compared to lower elevation (Churchland and Grayston, 2014; Veen et al., 2017). In contrast, the dominance of typical epi-edaphic species (*Isotoma anglicana*, *I. viridis*, and *Isotomurus graminis*) at 900 m in the meadow did not correspond with any of the measured soil biological or chemical characteristics or with vegetation composition. However, the increase in springtail abundance did coincide with low temperatures for both vegetation types. These findings show that temperature changes that occur with elevation can result in corresponding shifts in species dominance for springtail communities depending on vegetation type. Whether these differences result directly from selection for pioneer species via freezing temperatures (Hågvar and Pedersen, 2015), or indirectly through changes in the microbial community and litter layer that they inhabit (Erhagen et al., 2013; Tybirk et al., 2000), would require further investigation.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.pedobi.2018.02.004.

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